POST-LARVAL CHANGES IN THE VERTEBRAL ARTICULATIONS OF SPELERPES AND OTHER SALAMANDERS.

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In defining the minor subdivisions of the Urodela, Cope and Boulenger have given fundamental importance to the form of the vertebral central articulations. Cope ('89, p. 33, and earlier papers) arranges the families of Pseudosauria in two series, the one characterized by amphicœlous, the other by opisthocœlus vertebræ, and on p. 190 he states that the peculiarity of the vertebræ chiefly distinguishes the Desmognathidæ from the Plethodontidæ. Boulenger ('82, p. 2), whose subfamilies of salamanders have nearly the same content as Cope's families, mentions the form of the central articulations as the sole distinguishing feature between his Plethodontinæ and Desmognathinæ.

Apparently the only serious criticism of the value of this character has been made by Vaillant, who in a short note ('84) describes the vertebræ of *Autodax* (*Anaides*) *lugubris* as opisthocœlous. Boulenger, after an examination of the dissection made by the French zoölogist, characterizes ('85) this statement as erroneous. In a second note ('86) Vaillant explains the reason for this difference of opinion and reiterates his former statement. The vertebræ in question he describes as osteologically amphicœlous but physiologically opisthocœlous, meaning by this that if the actual bone tissue alone be considered the centra are biconcave ; but that the anterior cup is filled by a cartilaginous nodule, which projects freely in the form of a hemipshere whose free surface fits into the posterior socket of the preceding vertebra.

If a full-grown larva of *Spelerpes ruber* be examined, the vertebral centra will be found to be very deeply concave. The apices of the two cone-shaped cavities almost meet at the middle of the vertebra, where they communicate through a small foramen through which the here constricted notochord passes. The cavities are largely occupied by the notochord, which suffers a second (intervertebral) constriction due to an annular thickening of the car-

tilaginous notochordal sheath by which contiguous vertebræ are bound together.

After the metamorphosis, when the young salamander has a length of 90–100 mm., this cartilaginous ring increases in thickness and extent so that it largely replaces and constricts the notochord. The cartilage becomes firmer and may be removed in its entirety as a fusiform nodule bearing fragments of the notochord at its ends. If the vertebral column, either in its fresh state or after preservation in alcohol, be bent sharply so that it parts intervertebrally, this nodule will remain attached indifferently either to the anterior or posterior contiguous vertebra.

Gradually the cartilage extends, encroaching more and more on the notochord, and at the same time its posterior peripheral parts begin to calcify, first in a post-equatorial zone which lies just within the rim of the anterior cup of the succeeding vertebra. In individuals having a length of 120 mm.[1] this calcified ring is already quite conspicuously developed and has united with the anterior vertebral rim. Dried skeletons of this stage show the anterior vertebral cup with a thick, rather rough rim and a correspondingly constricted opening, while the posterior cup remains almost exactly of its previous form and proportions. Its opening is large, unconstricted and has a smooth, thin margin which embraces the next succeeding centrum; its inner surface is bounded everywhere by hard, true bone lined by a thin layer of cartilage. Moreover, if the column be forcibly broken as described above, the cartilaginous nodule almost invariably parts from the preceding and remains attached to the succeeding vertebra, showing its more intimate organic union with the latter. A smooth articulation between this cartilage and the posterior face of the preceding vertebra begins to be evident and the contiguous centra are united by an annular intervertebral ligament. A condition closely approximating that just described is figured by Wiedersheim ('93, p. 61, fig. 41,C.).

With increasing age and size the calcified area continues to encroach on the cartilaginous matrix. The ring becomes thicker and its posterior margin extends toward the middle region of the centrum. As a result the anterior cavity of the bony vertebra grows

[1] As there appears to be some individual variation in the rate of change, the conditions described must be understood as belonging to individuals of only approximately the lengths stated.

smaller as it is filled up from the bottom and sides by the gradual replacement of true cartilage by calcified cartilage. To a corresponding degree the cartilaginous nodule becomes incorporated with the succeeding vertebra and structurally separated from the preceding one. In ordinary breeding individuals, having a length of 130–150 mm., is reached the condition which Vaillant has happily described as physiologically opisthocœlous, in which the actual intervertebral centre of movement is between a cartilaginous ball structurally united with the anterior end of one vertebra and a deep cup borne on the posterior face of the other. There is no synovial articulation formed at this stage but only a curved surface of fracture which divides the intervertebral cartilage.

In still larger individuals, up to a length of 170 mm., which are not rare, the process of calcification has extended all through the cartilage within the anterior vertebral cup, at first leaving here and there little lakes of unaltered cartilage, which are finally also affected by the change. The transformation of tissue then overflows the boundaries of the cup, first at the rim, but gradually extends into the centre and anterior superfices of the cartilaginous head. At this period of development the unchanged cartilage has been reduced to a cap which fits over a rounded calcified head of its transformed substance and becomes constantly reduced in thickness as the process of calcification extends. If the cartilage be scraped away or shrunken by complete drying a larger or smaller central depression appears in the anterior face of the vertebra at the point where the notochord and its cartilaginous envelope longest persist.

Finally, in the very largest individual which I have seen, which, if the tail were complete, would measure upward of 180 mm., the vertebræ are quite as opisthocœlous as even in the largest individuals of *Desmognathus*. The anterior ball has become, with the exception of a thin articular surface such as persists in all opisthocœlous salamanders, completely calcified and as hard and dense as the body of the vertebra. So far as microscopical examination has extended, this calcified tissue does not become true bone. In sections after removal of the lime salts the original cartilage, except for the rearrangement of the cells, remains in a nearly unaltered state. In many of the larger specimens the annular intervertebral ligament ossifies, beginning at its anterior

attachment and extending caudad. By this means the rim of the posterior cup is built up higher and the socket deepened. Between the overlapping vertebral rims an annular synovial sac is developed.

Whether the vertebræ of *Spelerpes ruber* are properly designated as amphicœlous or opisthocœlous depends, therefore, on the age of the individual under consideration, and whether attention is directed to the bony parts only or to the cartilage as well. During late larval life and for a time after the metamorphosis, the vertebræ are both osteologically[2] and physiologically amphicœlous. During the prime of life they are still amphicœlous so far as the strictly bony portions of the centra are concerned; but if, as seems more logical, the cartilaginous structures also are considered they cannot be characterized otherwise than as opisthocœlous. In old age they are opisthocœlous in every sense in which that term can be applied to the vertebræ of *Desmognathus*. Developmental progress in the structure of the vertebræ from a primitive to a more specialized type is continuous throughout life.

It is well known that the amphicœlous condition of the vertebræ of the higher salamanders is attained by a course of development essentially similar to what has just been described for *Spelerpes*. The examination of a large series of *Desmognathus fusca* and *D. nigra* shows that this is true of these species. The species of *Desmognathus* transform when of much smaller size relatively to the limit of growth than those of *Spelerpes*. The just transformed *D. fusca* is about one-half the length of *S. ruber* at a corresponding period, although the breeding adults are only about twenty per cent. inferior. Calcification of the intervertebral cartilage proceeds quite rapidly, so that individuals of 50–60 mm. are in the same stage as *Spelerpes ruber* of 135–140 mm. Even before attaining a length of 100 mm. the vertebræ are as strictly opisthocœlous as in the largest *S. ruber*, and have attained that condition by a similar series of steps. It is noticeable that the calcified material of the ball is softer than the fully ossified portions of the vertebræ, and that small enclosures of unchanged cartilage may persist, as well as a remnant in the centre of its free surface, where a depression appears in the dry skeleton. The later development consists simply in the completion of calcification.

[2] Used in the sense of Vaillant in the papers cited, and of some systematists to denote the condition of actual bone and calcification.

The vertebræ of the two forms now under consideration do not properly belong to two types, but differ only in the period of life at which the steps in development are passed through and at which the higher structural type is attained. The completely osseous opisthocœlous condition is reached in *Desmognathus fusca* prior to the period of maturity and reproduction, in *Spelerpes ruber* only after that period.

It seemed desirable to ascertain whether these conditions are general among the genera of the more primitive families of the Pseudosauria.[3] As it was important to mutilate most of the material as little as possible, but a single articulation was generally exposed and studied on each specimen, and for the sake of uniformity this was always the same one, the fifth anterior to the sacral vertebra being selected for various reasons. The following notes show the character of typical genera:

AMBLYSTOMIDÆ.

The largest available specimens of *Amblystoma opacum*, *A. tigrinum*, *A. punctatum* and *A. jeffersonianum* were examined without the detection of any changes of the nature sought. Throughout life the vertebræ appear to remain deeply and equally amphicœlous and the intervertebral cartilage to undergo no calcification.

Chondrotus tenebrosus.

It was fully expected that this species, because of its large size and robust build, might present calcified intervertebral cartilages, but even an unusually large individual (282 mm.) remains in the simplest amphicœlous condition. The two faces of the centrum are equally and very deeply cupped. The notochord is largely persistent. The intervertebral thickening of the cartilaginous sheath is slight and extends into the concavities of the contiguous vertebræ, from which it may be easily removed without injury.

PLETHODONTIDÆ.

The very small species of this family will require to be studied by means of sections, but the following will illustrate the conditions met with :—

[3] This I have been enabled to partially do chiefly through the courtesy of the Curators of the Academy of Natural Sciences of Philadelphia, and especially of the Conservator of Vertebrata, Mr. Witmer Stone, who placed at my disposal the extensive collections of that institution.

Hemidactylium scutatum.

The largest specimens examined measure 80–85 mm. and are strictly amphicœlous.

Plethodon cinereus.

Always strictly amphicœlous. This species and the next are among those which show that neither a terrestrial habit nor a long period of growth between metamorphosis and maturity is the determining factor in the complete calcification of the articular head.

Plethodon glutinosus.

Many specimens of this species were examined, including two large ones of 167 mm. and 177 mm., belonging to the collection at the Academy. All have deeply biconcave vertebræ without any visible sign of calcification of the intervertebral cartilage, though in the larger individuals it is evidently more firmly attached to the succeeding than the preceding vertebra. Although there is no fully formed articulation, a definite curved surface of fracture corresponding to one is developed.

Plethodon æneus. Plethodon oregonensis.

Both amphicœlous. Of the former the largest specimen examined measured 164 mm.; in this the whole body of the vertebra appears to be somewhat imperfectly ossified.

Autodax lugubris.

In two examples of 90 mm. and 105 mm. length the vertebræ are biconcave, with the intervertebral cartilage unmodified and most strongly attached by the articular ligaments to the anterior vertebra. The intervertebral articulation is developed. Two others of about 145 mm. have the posterior face deeply cupped, the anterior, after removal of the cartilage, much more shallow and rough from the development of calcified tissue. The uncalcified cartilage has a smooth surface which fits into the next anterior socket.

Geotriton fuscus.

Only one small specimen of 86 mm. was available for dissection, and this was nearly equally amphicœlous, with the intervertebral cartilage remaining attached to the posterior face on being fractured. Murray ('97) has figured a section of a vertebra of this species which exhibits no modification of the cartilaginous inter-

vertebral ring. Probably older specimens would show changes similar to *Spelerpes ruber*.

Œdipus variegatus.

One with the tail missing and the body measuring 45 mm. in length has the anterior face slightly less cupped than the posterior, and retaining the intervertebral cartilage. In two specimens of 145 mm. and 147 mm. the anterior cup is about one-third filled with calcified cartilage.

Gyrinophilus porphyriticus.

A larva of 78 mm. has the bony centra deeply biconcave, the notochord largely persistent but constricted by a narrow but rather thick intervertebral cartilaginous ring.

A specimen of 106 mm., probably recently metamorphosed, exhibits a much more extensively developed intervertebral cartilage, but appears to be unchanged otherwise.

In one of 133 mm. the notochord is still largely persistent, the intervertebral articulation has formed in the cartilage as a curved plate of flattened cells and the widely flaring posterior rim of the bony centrum begins to overlap and embrace the more constricted anterior rim. This is nearly the stage figured by Wiedersheim.

One of 172 mm. shows a slight annular calcification of the intervertebral cartilage within the anterior cup.

In individuals of larger size the process of calcification is rapid. One measuring 185 mm. has the anterior cup filled flush to the brim with calcified tissue which presents a rough, nearly flat surface when the cartilaginous head is scraped away. The largest specimen examined measured 200 mm., and in this the calcification extends slightly beyond the cup's rim.

Spelerpes bellii.

This large species probably undergoes intervertebral calcification, if at all, relatively later than *S. ruber*. In specimens of 180 mm. and 240 mm. no trace of calcareous infiltration could be detected. In both cases the intervertebral cartilage is more firmly attached by the articular ligaments to the anterior vertebra than by direct union to the posterior one.

Spelerpes longicudus.

Of all the species of Plethodontidæ examined this appears to be the most precocious in respect to the feature under consideration.

In an example measuring only 90 mm. calcification has already progressed so far as to fill about one-half of the anterior cup, and in one of 135 mm. the cup is filled to the brim, leaving only a very slight central depression.

Spelerpes bilineatus. Spelerpes guttolineatus.

Exhibit changes similar in character but somewhat more tardy in the time of their appearance.

DESMOGNATHIDÆ.

Typhlotriton spelæus.

The vertebræ of a 90 mm. example of this interesting blind salamander, of which only slightly larger specimens have been taken, are in about the same condition as those of a 60 mm. *D. fusca*, and consequently opisthocœlous only in the sense in which a mature *Spelerpes ruber* is opisthocœlous.

Desmognathus nigra.

Similar to *D. fusca*, but somewhat more retarded in development.

Leurognathus marmorata.

Of this species only a single skeleton of a length of 117 mm. has been examined. It differs from *Desmognathus* only in the greater prominence of the articular head.

Of the Salamandridæ and Pleurodelidæ no specimens were examined in this connection, as the vertebræ are well known through the researches of Wiedersheim ('75) and others to be strongly opisthocœlous and to ossify early.

When recourse is had to sections of a sufficient series of stages, other interesting changes and generic differences will no doubt appear ; but from the study of gross features alone it becomes evident that as regards the form of the vertebral articulations the genera of the families of salamanders present an unbroken developmental series.

The Amblystomidæ are probably always amphicœlous throughout life.

Within the Plethodontidæ the genera arrange themselves in two groups, the one including *Plethodon* and *Hemidactylium*, the other *Spelerpes*, *Gyrinophilus*, *Autodax* and *Œdipus*. The *Plethodon* group remains in the primitive state with little or no post-larval calcification of the intervertebral cartilages. The members of the *Spelerpes* group all (*S. bellii ?*) tend toward the opisthocœlous con-

dition, and earlier or later in life the intervertebral cartilages are affected by a process of calcification which is progressive and may finally involve the entire substance of the articular heads. It may be observed that the grouping of the genera as suggested, with the exception of *Autodax*, is confirmatory of Cope's view of their affinities.

Desmognathus and its allies arrive at the final opisthocœlous stage much earlier but by a series of post-larval stages quite similar.

Many peculiar structural features segregate the amphicœlous Amblystomidæ, on the one hand, and the opisthocœlous Salamandridæ and Pleurodelidæ, on the other, into distinct family groups. The failure of the only important character which has seemed to make the family distinction of the Plethodontidæ and Desmognathidæ desirable renders their separate continuance no longer necessary. Although *Leurognathus* resembles *Desmognathus* in the absence of a prefrontal bone in the adult, this is a very doubtful character, and in any case would probably have, with the peculiarities of the tongue, no more than subfamily value. The family should retain the prior name of Plethodontidæ. It seems to represent a phyletic line connected directly with the lower amphicœlous salamanders ; and distinct from the Amphiumidæ, on the one hand, and the Pleurodelidæ and Salamandridæ on the other.

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